

Locomotor Adaptations Reflected in the Wrist Joints of Early Tertiary Primates (Adapiformes)

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ABSTRACT The positional behaviors inferred for early Tertiary adapiform primates have been the subject of considerable debate. Adapiform wrist morphology is analyzed here within the context of extant morphoclines in carpal joint shape in order to reconstruct adapiform positional behavior. Extant vertical clingers, slow climbers, and arboreal quadrupeds differ significantly from one another in length of the m. flexor carpi ulnaris lever arm, shape of the midcarpal joint articular surface, and size and divergence of the pollical carpometacarpal articulation. These morphological differences are functionally related to differential requirements for wrist flexion, midcarpal mobility and stability, and pollical grasping, respectively. *Adapis*, *Notharctus*, and *Smilodectes* share with living arboreal quadrupeds a tall pisiform body, a mediolaterally flat midcarpal joint surface, and a relatively unexpanded thumb joint. Functionally, these features are related to flexing the wrist from extended positions during palmigrade, quadrupedal locomotion, increasing midcarpal joint stability during quadrupedal, weight-bearing postures, and grasping arboreal supports of predominantly horizontal and oblique orientation. The Messel adapiform (genus indet.) shares certain features of the midcarpal and pollical carpometacarpal articulations with extant vertical clingers, suggesting that this taxon used vertical substrates more frequently than other adapiforms. © 1996 Wiley-Liss, Inc.

PREVIOUS STUDIES OF ADAPIFORM POSTCRANIAL MORPHOLOGY AND POSITIONAL BEHAVIOR

Approximately 50 million years ago an adaptive radiation of early primates took place in North America and Europe. These early primates fall roughly into two groups, the small-bodied omomyiforms and the larger adapiforms (Covert, 1986). One of the more outstanding debates regarding the biology of these early primates concerns the positional behaviors characteristic of adapiform primates. Though a large sample of adapiform postcranial remains exists, postural reconstructions based upon study of these materials have often differed (for a thorough review see Dagosto, 1993).

For example, limb proportions of the North American notharctines are quite similar to those of extant vertical clingers (Napier and Walker, 1967). Postcranial remains of *Smilodectes gracilis* exhibit features of the shoulder (Covert, 1985a,b; Schmitt, 1991, in press) and elbow (Szalay and Dagosto, 1980) which also resemble those of extant large-bodied Malagasy vertical clingers, whereas morphology of the knee (Dagosto, 1993) and intertarsal articulations (Gebo, 1985) are reminiscent of more quadrupedal lemurs.

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Likewise, the elbow (Szalay and Dagosto, 1980), shoulder (Schmitt, 1991, in press), and elongate digits (Stern and Oxnard, 1973) of *Notharctus* are quite similar to those of extant vertical clingers, although the carpal (Godinot and Beard, 1991) and tarsal (Gebo, 1985) articulations have been compared favorably with those of more quadrupedal lemurs. The long bones of the European adapid *Adapis parisiensis* are quite similar in general proportions to those of the lorissine slow climbers (Dagosto, 1983), whereas the *Adapis* hand (Godinot and Jouffroy, 1984; Godinot, 1991, 1992) resembles that of essentially quadrupedal monkeys in certain respects. A virtually complete postcranial skeleton of an adapiform from Messel, Germany, appears to be that of a leaping primate with powerful grasping extremities (Franzen, 1987).

Virtually complete fossil carpal remains of the adapiforms *Notharctus tenebrosus* (Hamrick and Alexander, in press), *Smilodectes gracilis* (Beard and Godinot, 1988), *Adapis parisiensis* (Godinot and Jouffroy, 1984), and the Messel specimen (gen. indet.) (Franzen, 1987, 1993) are now known. Earlier (e.g., Lewis, 1974; Cartmill and Milton, 1977; Jenkins, 1981; Sarmiento, 1988) and more recent (Hamrick, 1995, 1996) studies of carpal joint structure and function in extant primates have shown that interspecific variation in carpal joint morphology is often functionally related to interspecific variation in positional behavior. Perhaps more so than any other postcranial region, the hand and wrist reflect locomotor and prehensile adaptations to the environment (Jouffroy and Lessertisseur, 1979). The primary objective of this study is to test previous locomotor and postural reconstructions for adapiform primates by analyzing adapiform carpal morphology within the context of extant morphology-function-behavior correlations.

WRIST JOINT MORPHOLOGY AND FUNCTION IN EXTANT PRIMATES

Neontological studies of hand structure and function in arboreal primates show that variation in carpal joint morphology tracks gross variation in locomotor and postural modes. Extant primate quadrupeds have an

elongate, rod-like pisiform which increases the moment arm for m. flexor carpi ulnaris (FCU) (Sarmiento, 1988) (Fig. 1A). Experimental studies (Whitehead, 1993) have shown that the FCU flexes the wrist from extended (= dorsiflexed) postures during the support (propulsive) phase of quadrupedal strides. The FCU inserts onto the base of the pisiform, and the FCU moment arm equals the distance between its insertion point and the center of the ulnocarpal joint. An elongate pisiform body increases the moment arm of this muscle by placing its insertion further away from the joint center (Sarmiento, 1988). Quadrupedal primates also subject the midcarpal joint to compressive, weight-bearing loads transmitted from the forelimb to the carpus during pronograde postures (Schön and Ziemer, 1973; Jenkins and Fleagle, 1975; O'Connor, 1975; Sarmiento, 1988; Hamrick, 1995, 1996). These taxa have a mediolaterally (= radioulnarly) flat curvature of the convex midcarpal joint surface so that the joint remains stable during compressive loading (Sarmiento, 1988; Hamrick, 1996) (Fig. 1A). Furthermore, quadrupedal taxa also possess a palmarly directed hamate "spiral" facet so that the midcarpal joint is impacted in an ulnarly deviated, extended, and pronated position (Lewis, 1974, 1989; Ziemer, 1978; Jenkins, 1981; Hamrick, 1996). Thus, habitually quadrupedal taxa are expected to have a tall pisiform body, relatively flat (mediolaterally) midcarpal joint articular surface, and palmarly directed triquetrohamate facet (Fig. 1A).

Vertical clingers require powerful grasping hands to maintain contact with vertical arboreal supports. These taxa have a divergent, elongated pollex so that the thumb can both subtend vertical substrates of variable diameter and generate a powerful adduction force normal to the substrate's surface in order to maximize friction and maintain contact (Cartmill, 1974, 1985; Hamrick, 1996) (Fig. 1B). Prolonged contraction of both the extrinsic pollical and intrinsic thenar eminence muscles during vertical clinging should produce considerable transarticular compressive forces across the pollical carpometacarpal joint. Joint stress resulting from these forces is reduced by expanding the con-

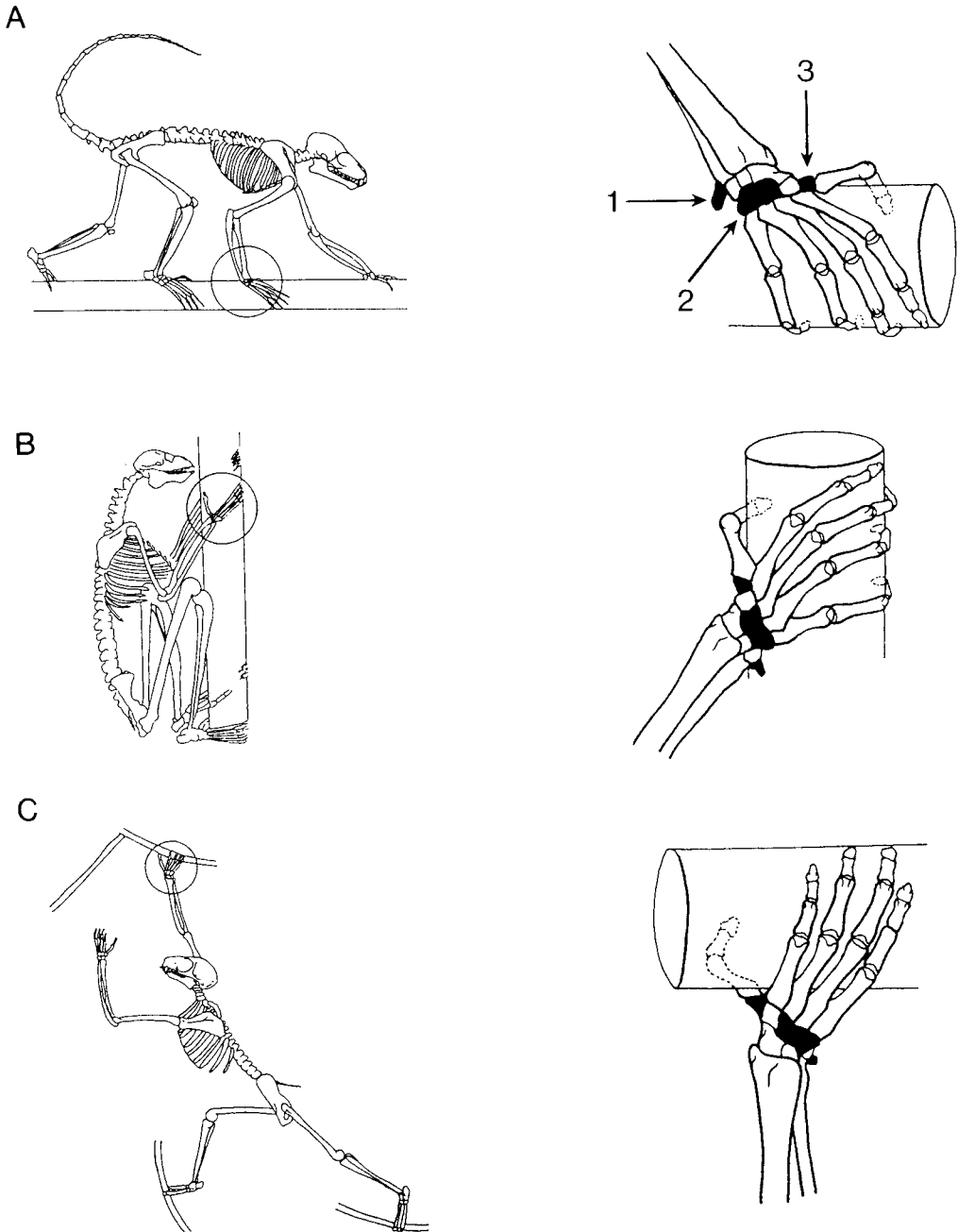


Fig. 1. Schematic representations of hand postures in a strepsirhine quadruped (**A**), vertical clinger (**B**), and slow climber (**C**). Arrows point to the pisiform (1), midcarpal joint (2), and pollical carpometacarpal joint (3). The pisiform, midcarpal articular surface, and trapezium are shaded. Insets A and B are redrawn from Fleagle (1988).

tact area at the pollical carpometacarpal articulation (Fig. 1B). The frequent use of orthograde postures by vertical clingers means that the midcarpal joints of these primates are not subjected to compressive, weight-bearing loads like the wrist articulations of arboreal and terrestrial quadrupeds (Fig. 1B). Furthermore, the midcarpal joint is impacted in a partially supinated position (Hamrick, 1996), so the hamate has a more dorsally extended articular surface for the triquetrum than that of quadrupeds. Hence, vertical clingers are expected to have both a divergent and expanded pollical carpometacarpal articulation, more mediolaterally curved midcarpal articulation, and some dorsal extension of the triquetrohamate facet (Hamrick, 1996) (Fig. 1B).

Finally, the slow-climbing form of locomotion practiced by lorises, in which two or more limbs are always in contact with the substrate, is characterized by extremely acrobatic forelimb postures (Charles-Dominique, 1971, 1977; Dykyj, 1980; Ishida et al., 1983, 1992; Jouffroy, 1989). Lorises maintain a secure grasp with one hand as the other reaches for variably oriented branches during climbing and bridging behaviors, which requires both axial rotation and radioulnar deviation at the wrist so that the forelimb and body can move about the fixed hand (Cartmill and Milton, 1977; Jouffroy, 1989) (Fig. 1C). During slow quadrupedal locomotion, the lorisine forelimb is protracted to such a degree that the forearm is parallel with the substrate and the hand is placed in an extremely ulnarly deviated position (Jouffroy et al., 1983; Ishida et al., 1992). Acrobatic slow climbers are therefore expected to have both a tightly curved midcarpal articular surface which increases their range of midcarpal radioulnar mobility (Yalden, 1972) and a dorsally extended triquetrohamate facet which increases their range of midcarpal rotation (Fig. 1C). Orthograde locomotor behaviors appear to require a greater range of carpal joint movement than orthograde postural behaviors (Hamrick, 1996), and slow climbers are expected to have a greater degree of midcarpal joint curvature than vertical clingers in order to increase their range of radioulnar wrist joint mobility during cautious climbing. Finally,

lorises use a powerful "pincer grasp" to securely clasp arboreal supports with the hand (Forster, 1933, 1934; Ishida et al., 1992; Jouffroy, 1993), which requires a divergent pollex to both increase the range of thumb abduction and enable the pollex to move transversely across the thumb when it is flexed. Thus, slow climbers are expected to possess an expanded and divergent pollical carpometacarpal articulation related to their powerful grasping thumb.

MATERIALS AND METHODS

Sample

The biomechanical relationships described above between carpal morphology and positional behavior in extant arboreal quadrupeds, vertical clingers, and slow climbers allow very specific predictions to be made regarding the carpal joint morphologies related to these positional behaviors in fossil primates. Correlations between wrist morphology, function, and positional behavior were first tested in a large sample of living taxa prior to qualitative and quantitative analyses of fossil specimens. A sample of 22 species was classified a priori into four broadly defined locomotor categories for morphometric analysis (Table 1). These locomotor groups are 1) quadrupedal prosimians, which leap and run on predominantly horizontal and oblique supports, 2) vertical clingers, which use upright, orthograde postures on vertical arboreal supports, 3) acrobatic climbers (the lorisines), which use extremely varied but frequently orthograde climbing postures on oblique and vertical supports (Charles-Dominique, 1971), and 4) quadrupedal monkeys, which move using above-branch quadrupedal walking, running, and some leaping on horizontal and oblique supports (Fleagle, 1988; Oxnard et al., 1990) (Table 1). Quadrupedal monkeys are placed in a locomotor group separate from quadrupedal prosimians because previous authors (Godinot and Jouffroy, 1984; Godinot and Beard, 1991) have likened *Adapis* to pronograde monkeys more so than quadrupedal prosimians.

The fossil adapiforms studied are from collections of the American Museum of Natural History (AMNH), the United States Na-

TABLE 1. Sample sizes for species assigned to the locomotor groups included for comparative analysis of adapiform carpal joint morphology¹

Locomotor groups (N)	Individuals
Prosimian quadrupeds (6, 93)	
<i>Lemur variegatus</i>	19
<i>L. rubriventer</i>	8
<i>L. catta</i>	19
<i>L. fulvus</i>	20
<i>Otolemur crassicaudatus</i>	19
<i>Cheirogaleus major</i>	8
Vertical clingers (6, 107)	
<i>Lepilemur mustelinus</i>	24
<i>Propithecus diadema</i>	16
<i>P. verreauxi</i>	22
<i>Indri indri</i>	22
<i>Avahi laniger</i>	13
<i>Galago senegalensis</i>	10
Slow climbers (4, 49)	
<i>Loris tardigradus</i>	8
<i>Nycticebus coucang</i>	20
<i>Arctocebus calabarensis</i>	4
<i>Perodicticus potto</i>	17
Anthropoid quadrupeds (6, 29)	
<i>Saimiri sciureus</i>	6
<i>Aotus trivirgatus</i>	5
<i>Alouatta palliata</i>	4
<i>Cercopithecus mitis</i>	6
<i>Miopithecus talapoin</i>	4
<i>Macaca spp.</i>	4

¹ Numbers in parentheses refer to the number of species and the number of individuals, respectively, for each locomotor group.

tional Museum (USNM), the private collection of Msr. A. Collier (RD), and the Senckenberg Museum (SMF). These fossils include virtually complete hand and forelimb remains of *Notharctus tenebrosus* (AMNH 127167) (Hamrick and Alexander, in press), *Smilodectes gracilis* (AMNH 13251) (Beard and Godinot, 1988), *Adapis parisiensis* (RD 311) (Godinot and Jouffroy, 1984), and the Messel adapiform (gen. indet.) (SMF-ME 1683) (Franzen, 1987), which were initially described by the aforementioned authors. The temporal and provincial affinities of each fossil specimen are not treated here.

Measurements

A series of linear and angular measurements were used to quantify variation in the bony carpal joint dimensions discussed above. Specifically, these measurements quantify length of the m. flexor carpi ulnaris moment arm, transverse curvature of the midcarpal joint articular surface, size of the trapezium–first metacarpal joint, and thumb divergence (Fig. 2). Linear measurements include height of the pisiform body

and breadth of the trapeziometacarpal articular surface, and angular measures include mediolateral curvature of the midcarpal articulation and divergence of the trapeziometacarpal articulation (Fig. 2). Linear measurements were taken using dial calipers. Angular measurements were obtained by digitizing points on the carpal elements with a COMP 3D High Precision Reflex Microscope (Scott, 1991). Thumb divergence was determined by digitizing points on the distal trapezoid and trapezium metacarpal facets and then calculating the angle between lines formed by the points (after Godinot, 1992) (Fig. 2). Transverse curvature of the midcarpal joint was calculated using the method described by Hamrick (1996). This technique involves digitizing points on the midcarpal articular arc (Fig. 2) and then calculating the included angle which subtends a triangle inscribed within the articular arc (Fig. 2) (Hamrick, 1996). This angle is basically a means of expressing the height of the articular arc relative to the arc's chord length.

Statistical analysis

Several statistical approaches were used to test the morphoclines described for the extant primate locomotor groups (see Introduction; Table 1) prior to analyzing the fossil specimens. All statistical tests were performed on species means. Relative pisiform body height and trapezium articular breadth were initially expressed as shape ratios by dividing these measurements by a new size variable, termed carpal size, which is the geometric mean of thirteen linear dimensions taken on the distal, radius, ulna, and carpus. The shape ratios were then logged to create log-shape variables (Darroch and Mosimann, 1985; Falsetti et al., 1993). Non-parametric Kruskal-Wallis tests were used to identify log-shape variables and angular measures for which significant between-group differences exist, and Kolmogorov-Smirnov tests used for pairwise between-group comparisons.

Log-shape variables and angles were tested for correlations with size by generating both Spearman rank and Pearson correlation coefficients between these variables and carpal size (geometric mean). Correla-

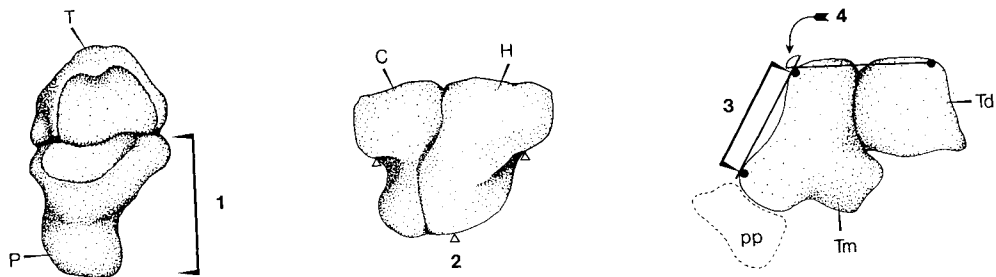


Fig. 2. Proximal view of the pisiform (P) and triquetrum (T) (**left**), dorsal view of the capitulum (C) and hamate (H) (**middle**), and dorsal view of the prepollex (pp), trapezium (Tm), and trapezoid (Td) (**right**) showing the carpal measurements included for analysis. Measurements include dorsoventral height of the pisiform body (1), mediolateral curvature of the midcarpal articular surface (2), breadth of the trapeziometacarpal articulation (3), and trapezium divergence (4). Measurements 1

and 3 are taken using dial calipers. Midcarpal curvature (2) is calculated by digitizing three points on the articular surface, indicated by triangles (middle), and deriving the angle which subtends a triangle inscribed within the three points (Hamrick, 1996). Trapezium divergence (4) is calculated by digitizing three points on the trapezium and trapezoid (right), indicated by closed circles (right), and deriving the angle between lines formed by the points (4).

tions were significant ($P < .05$) in most cases, and so analysis of covariance (ANCOVA) was used to test for between-group differences in linear and angular carpal dimensions relative to carpal size. The basic question asked in these analyses is whether or not Y is larger for one group than the other at similar values of X (= carpal size). Standard parametric methods are not always appropriate for these between-group tests, since the sample sizes are small and occasionally unequal (Plotnick, 1989). Therefore, Tsutakawa and Hewett's (1977) "quick test" was also used as a nonparametric bivariate approach to test for between-group differences in carpal joint dimensions (Fig. 2) relative to carpal size. The reduced major axis (RMA) (Clarke 1980) regression model was chosen for these tests because neither the X nor Y variable was measured without error (Harvey and Pagel, 1991). Results using both methods were found to be similar, and so only ANCOVA test results are presented here.

A multivariate discriminant analysis was also performed on the shape ratios and angles to further test for significant differences between the locomotor group centroids using the multivariate data set. A multivariate analysis of variance (MANOVA) was the preferred technique for this analysis since the locomotor groups were defined a priori (Neff and Marcus, 1980). Values were logged and transformed to Z-scores prior to analysis

so that the angles and ratios were expressed in units of comparable magnitude.

The fossil specimens were included for analysis after testing for significant differences in carpal morphology between the extant locomotor groups (Table 1). Specimens of *Notharctus*, *Adapis*, and *Smilodectes* are so complete that most of the measurements shown in Figure 2 could be obtained without difficulty. Trapezium divergence had to be estimated for *Smilodectes*, since no trapezoid is known for this genus. Trapezium divergence was calculated for this specimen by drawing the second metacarpal facet perpendicular to the trapezium's articular facet for the trapezoid. Thumb divergence was then calculated as the angle between the pollical carpometacarpal articular facet and the estimated distal trapezoid surface. The estimated thumb divergence value for *Smilodectes gracilis* is 213.3 degrees, which is virtually the same as that of *Notharctus tenebrosus*. The Messel specimen is partly damaged and preserved only in dorsal view, so only thumb divergence could be measured.

Several statistical approaches were used to assign the fossil specimens to a particular locomotor group. First, Model I linear regressions were performed for each extant locomotor group for the measurements shown in Figure 2. Model I regression, and not Model II, was chosen for these analyses since the line was fitted for the purpose of prediction

TABLE 2. Summary regression statistics for linear and angular carpal dimensions against carpal size for each locomotor group¹

Measurement	Locomotor group	Slope	Y intercept	r
Pisiform height	PQ	.92	.36	.92**
	AQ	.89	.63	.98
	VC	1.03	.08	.99
	CL	.91	.13	.99**
Midcarpal mediolateral curvature	PQ	-.97	95.6	.24 ns
	AQ	-9.91	98.93	.72*
	VC	-3.59	101.69	.52 ns
	CL	-4.29	113.27	.53 ns
Trapezium breadth	PQ	.96	.06	.98
	AQ	.99	-.04	.97
	VC	.99	.13	.99
	CL	.77	.53	.97*
Trapezium divergence	PQ	12.88	205.05	.48 ns
	AQ	-3.78	214.48	.42 ns
	VC	-15.67	246.45	.92
	CL	1.75	250.56	.08 ns

¹ AQ, anthropoid quadrupeds; CL, slow climbers; PQ, prosimian quadrupeds; VC, vertical clingers. r is the correlation coefficient. All correlations are significant at $P < .001$ unless otherwise noted.

* $P < .05$.

** $P < .01$.

ns, not significant.

(see below; Sokal and Rohlf, 1981; Smith, 1994). Only those regressions using linear dimensions as dependent variables were consistently significant (Table 2). Using each locomotor group regression equation, predicted pisiform height and trapezium breadth values, along with a 95% prediction interval, were generated for each fossil specimen based on its carpal size value. The actual pisiform height and trapezium breadth values of each fossil specimen were then compared with those predicted by each locomotor group regression equation in order to assign each specimen to a particular extant locomotor group. Second, in all univariate plots of angular variables, fossil specimens were plotted along with the median and range for each extant locomotor group. Finally, the fossil specimens were entered into the discriminant analysis as unknowns. Each individual fossil specimen was then assigned to one of the four extant locomotor groups (Table 1) based on its factor score.

RESULTS

Comparative morphology

Adapiform primates resemble one another in many aspects of wrist joint morphology but do show a few interspecific differences related to subtle contrasts in carpal joint function. Similarities in proximal wrist joint morphology observed among adapiforms in-

clude a dorsopalmarly expanded ulnotriquetral articulation and pisiform body. These features resemble those of extant arboreal, quadrupedal anthropoids and prosimians. The midcarpal joints of the notharctines, and *Adapis*, exhibit a relatively flat midcarpal joint surface, palmarly directed hamate spiral facet, and small hamate hamulus. These characteristics are also common among living arboreal quadrupeds, whereas the Messel adapiform has a more tightly curved midcarpal joint surface like extant vertical clingers. The pollical carpometacarpal articulation of adapiforms is slightly divergent relative to the second metacarpal facet but is not markedly expanded like those of living clingers and slow climbers.

The triquetrum's articular facet for the ulna is high dorsopalmarly and constricted mediolaterally in all adapiforms which preserve the morphology (Fig. 3). Hence, parasagittal movements appear to have been emphasized at the adapiform ulnotriquetral joint. Godinot and Beard (1991, p. 314) noted that the notharctine triquetrum bears a "nonarticular bony process of unknown function [which] protrudes from the ulnar side of the bone." Lemuriforms also possess this bony process, which does not articulate with the ulna but instead embraces the dorsal body of the pisiform (Fig. 3) (Hamrick, 1996). This bony flange is bound tightly to the pisi-

form by the ulnospisiform ligament and in living lemurs is also tethered securely to the distal ulna by the ulnotriquetral ligament (Hamrick, 1996). This osteoligamentous arrangement creates an extremely stable configuration for the tip of the ulna and in fact restricts the range of ulnar deviation at the ulnocarpal joint. The majority of radioulnar deviation at the lemuriform wrist occurs at the midcarpal joint (Hamrick, 1995, 1996). Adapiforms also possess a tall pisiform body (Beard and Godinot, 1988; Godinot and Beard, 1991; Franzen, 1993) (Fig. 3), comparable in relative size to that of extant lemurs (Fig. 3), which increases the moment arm for *m. flexor carpi ulnaris*. The flexor carpi ulnaris muscle flexes the wrist from extended (= dorsiflexed) postures during the support phase of quadrupedal locomotion (Jouffroy, 1991, 1993; Whitehead, 1993). Both the dorsoventrally expanded triquetral articular surface and pisiform body indicate that parasagittal movements were emphasized at the adapiform ulnocarpal joint.

Qualitative comparisons made here show that the midcarpal joints of the notharctines and *Adapis* resemble those of quadrupedal monkeys and lemurs in having an articular facet for the triquetrum which faces somewhat proximally in a weight-bearing attitude (Fig. 4). The proximally facing triquetral facet increases midcarpal joint stability under compressive, weight-bearing loads transmitted from the ulna to the carpus during quadrupedal postures (Jenkins and Fleagle, 1975; Fleagle, 1977; Sarmiento, 1988). This facet spirals ulnarly and palmarly (Fig. 5) so that the joint is impacted in an ulnarly deviated and pronated position during the support phase of quadrupedal locomotion (Lewis 1974, 1989). Beard and Godinot (1988), Godinot and Beard (1991), and Franzen (1993) observed that *Notharctus* exhibits a hamate spiral facet which faces proximally more so than that of other adapiforms, giving the joint a relatively flatter mediolateral curvature. The triquetrohamate facets of *Adapis*, *Notharctus*, and *Smilodectes* all face somewhat proximally and are quite similar to one another in orientation (Fig. 4) (Hamrick, 1996). I agree with Franzen (1993), however, that the Messel specimen differs from the other adapiforms

in having a more medially (rather than proximally) facing triquetrohamate facet, resembling extant vertical clingers in this respect (Fig. 4).

Adapiforms also have a very small hamulus on the hamate (Fig. 5). The hamulus is the ulnar anchor for the carpal tunnel and is extended palmarly in primates with a deep carpal tunnel and large digital flexors (e.g., extant vertical clingers and slow climbers) (Fig. 5). The small size of the adapiform hamulus suggests that these primates lacked the large digital flexors and deep carpal tunnel that characterize living quadrupedal strepsirrhines (Fig. 5). Godinot and Beard (1991) commented that the robust trapezium tubercle of adapiforms compensated somewhat for the short hamate hamulus and increased the depth of the carpal tunnel. Dissections performed on *Otolemur*, *Lemur*, and *Saimiri* in previous studies (Hamrick, 1995, 1996) revealed that the transverse carpal ligament attaches primarily to the hamate hamulus and scaphoid tubercle, whereas the trapezium tubercle contributes very little towards the effective depth of the carpal tunnel. Moreover, the adapiform trapezium tubercle was not observed to be any more well developed than those of the extant taxa studied. These observations underscore the fact that adapiforms exhibit a very shallow carpal tunnel for the long digital flexors. This suggests that the adapiform extrinsic flexors were not so well developed as those of extant strepsirrhine quadrupeds, clingers, and slow climbers.

Adapiforms all have a pollical carpometacarpal articular facet that is somewhat divergent relative to the trapezoid's facet for the second metacarpal (Fig. 6). Qualitative comparisons presented here show that the thumb joints of all adapiforms are roughly as divergent as that of *Lemur* (Fig. 6), although Gregory (1920) considered *Notharctus* to resemble living *Cebus* in having a less divergent thumb. Godinot (1991) also found *Adapis* to have a somewhat divergent pollical carpometacarpal articulation. The trapezium is larger than the trapezoid in all adapiforms examined except for *Notharctus*, which has an extremely large trapezoid (Fig. 6). The large trapezoid of *Notharctus* may be functionally related to greater compressive

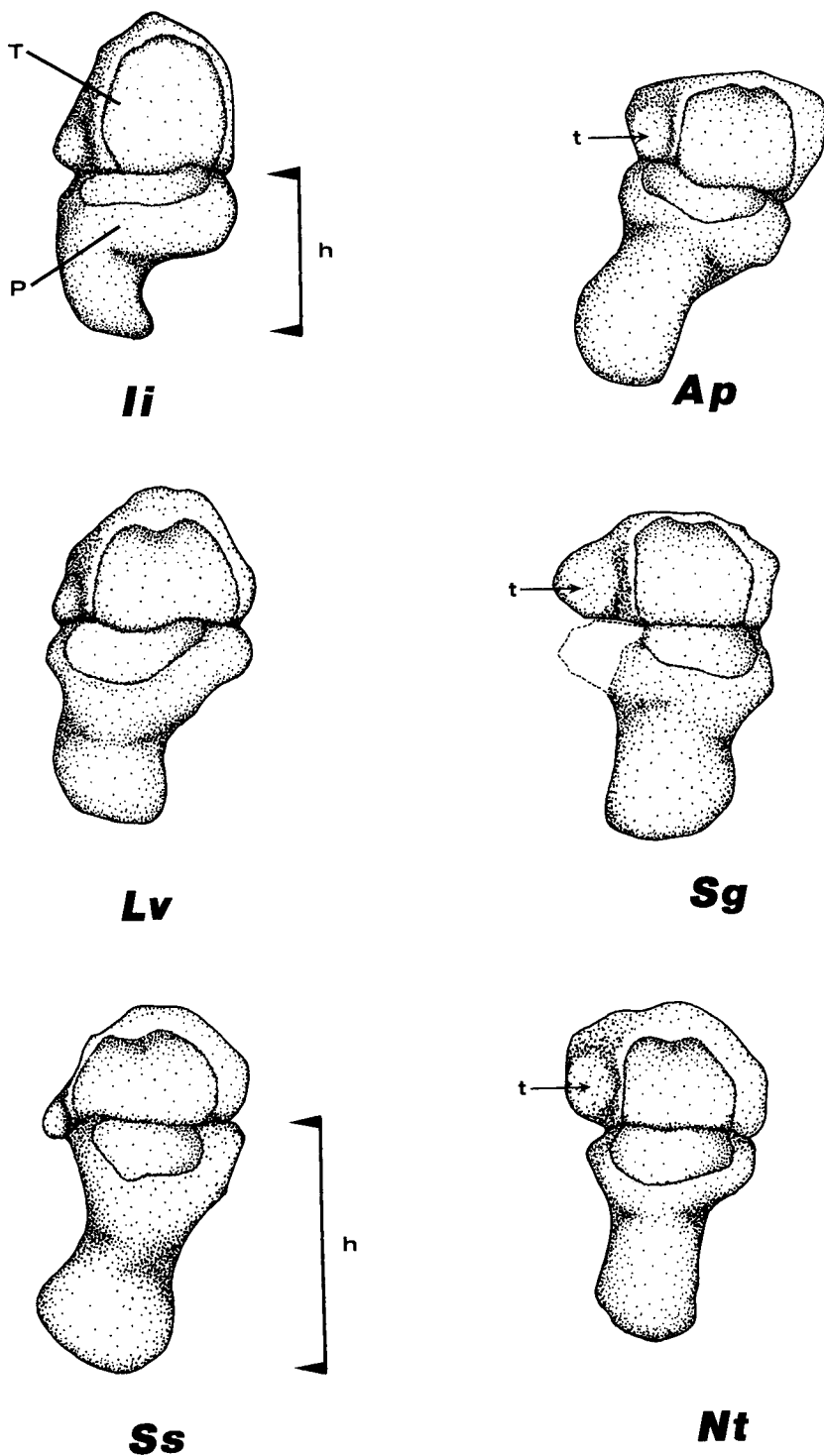


Fig. 3. Proximal view of the left triquetrum (T) and pisiform (P) of extant primates (**left column**) and adapiforms (**right column**) showing the short pisiform body (h) of *Indri indri* (Ii) and tall pisiform body (h) of *Lemur variegatus* (Lv) and *Saimiri sciureus* (Ss). Note that the fossil adapiforms *Adapis parisiensis* (Ap) (RD 311), *Smi-*

lodectes gracilis (Sq) (USNM 13251), and *Notharctus tenebrosus* (Nt) (AMNH 127167) have a tall pisiform body. Note also the large ulnar tubercle (t) for insertion of the ulnotriquetral ligament in the adapiforms. Not to scale.

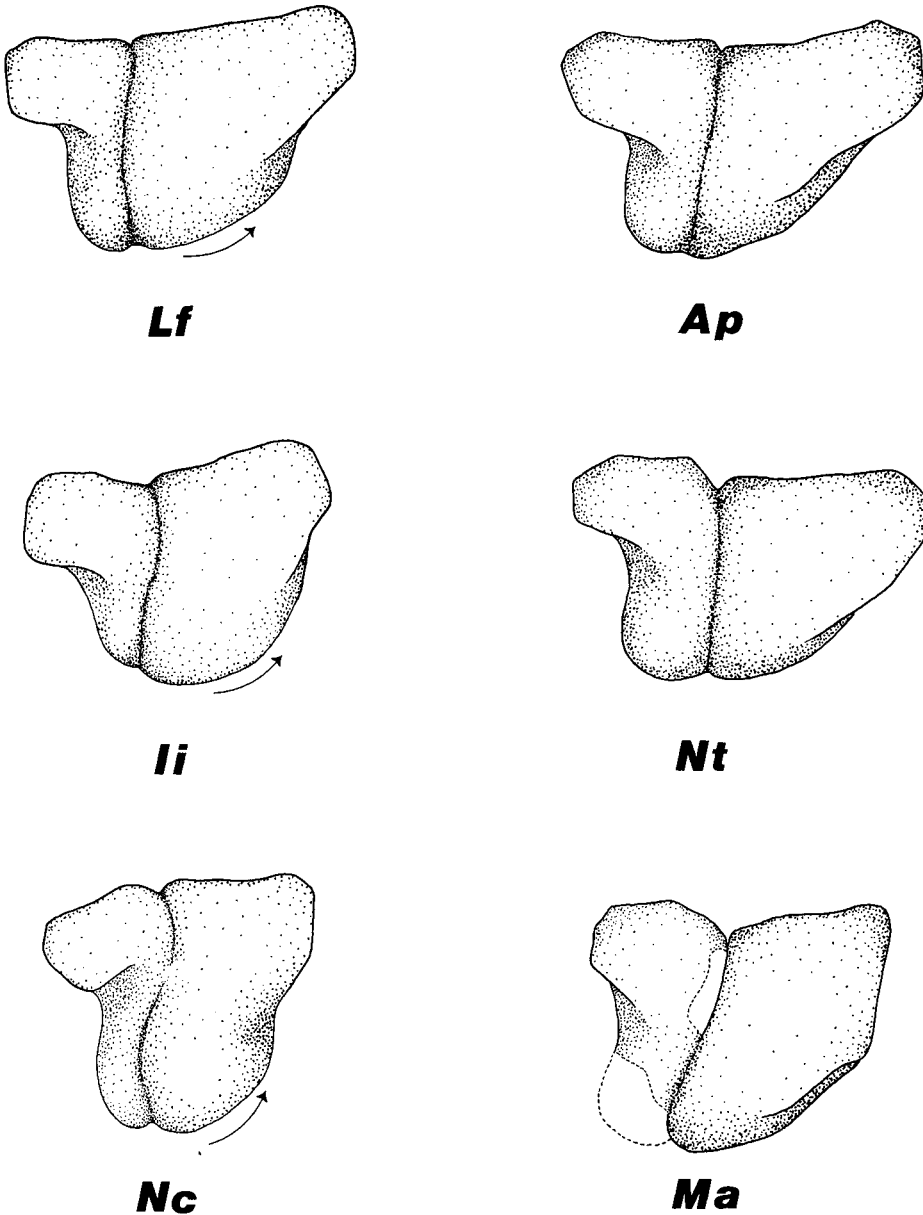


Fig. 4. Dorsal view of the distal midcarpal joint surface of extant primates (**left column**) and adapiforms (**right column**). Note the tight mediolateral (= radioulnar) curvature of the joint in *Nycticebus coucang* (arrow) (*Nc*), *Indri indri* (arrow) (*Ii*), and the Messel

adapiform (*Ma*) (SMF-ME 1683). The joint surface is relatively flatter in *Lemur fulvus* (arrow) (*Lf*) and the adapiforms *Adapis parisiensis* (*Ap*) (RD 311) and *Notharctus tenebrosus* (*Nt*) (AMNH 127167) due to their proximally facing triquetral facet. Not to scale.

loading along the long axis of the second digit compared to other adapiforms (Hamrick and Alexander, in press). Comparisons between adapiforms and extant primates show that

adapiforms lack the expanded first metacarpal facet and reduced second metacarpal facet characteristic of vertical clingers and climbers but instead resemble more quadru-

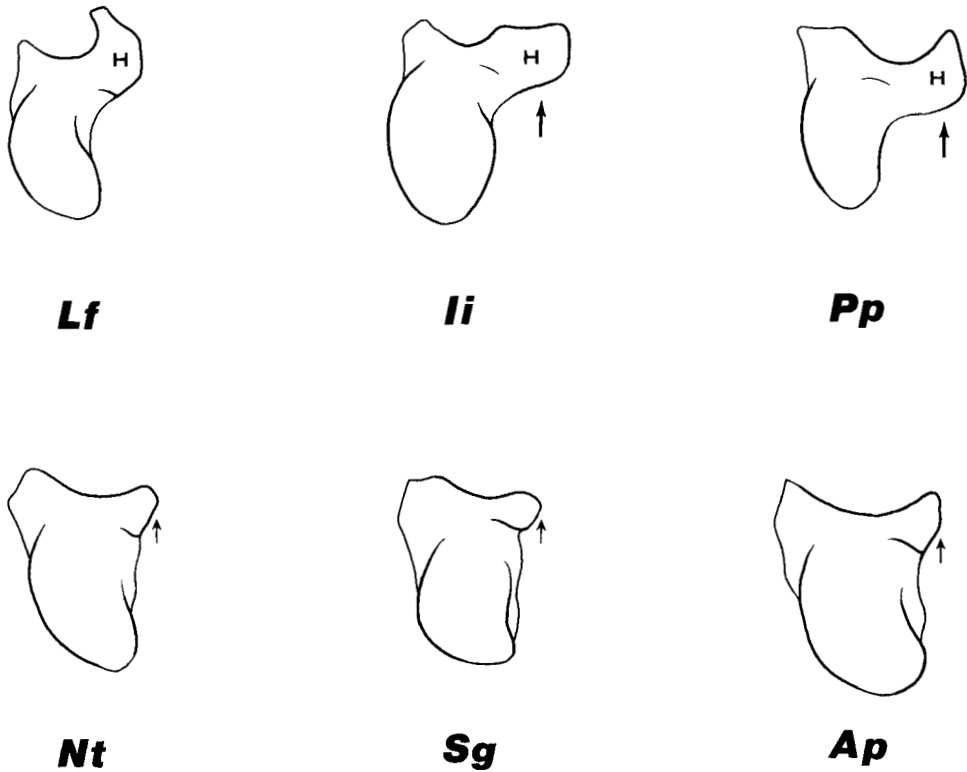


Fig. 5. Ulnar view of the hamate and hamate hamulus (H) in extant primates (**top row**) and adapiforms (**bottom row**). Note the elongate, palmarly projecting, hamulus of *Perodicticus potto* (arrow) (*Pp*) and *Indri indri* (arrow) (*Ii*) and relatively shorter hamulus (arrow) of *Lemur fulvus* (*Lf*) and the adapiforms *Notharctus tenebrosus* (*Nt*) (AMNH 127167), *Smilodectes gracilis* (*Sg*) (USNM 13251), and *Adapis parisiensis* (*Ap*) (RD 311). Not to scale.

pedal monkeys and lemurs in thumb joint morphology (Fig. 6).

These qualitative differences in carpal joint morphology between adapiforms and extant primates suggest that these fossil taxa possessed little potential for radioulnar deviation at the ulnocarpal joint, but shared a powerful moment arm for *m. flexor carpi ulnaris*. The adapiform ulnocarpal joint was primarily uniaxial and was probably frequently extended during some form of quadrupedal locomotion. The adapiform midcarpal joints, with the exception of the Messel specimen, resemble those of extant quadrupedal prosimians and anthropoids in having a palmarly directed and proximally facing triquetral articular facet on the hamate. This suggests that the midcarpal joints of these species, like those of living arboreal quadru-

peds were impacted in a slightly ulnarly deviated and pronated position (Lewis, 1974, 1989; Hamrick, 1996). The more medially facing triquetrohamate facet, and therefore more tightly curved midcarpal articulation, of the Messel specimen implies more frequent use of orthograde postures by individuals of this species. The hamate hamulus of adapiforms is also quite small, indicative of a shallow carpal tunnel for digital flexors that were not so well developed as those of living clingers and slow climbers. Finally, adapiform thumb joints are quite similar to those of extant arboreal, quadrupedal primates in terms of their divergence and relative size.

Comparative osteometrics

Bivariate and univariate analyses demonstrate that a strong morphocline exists

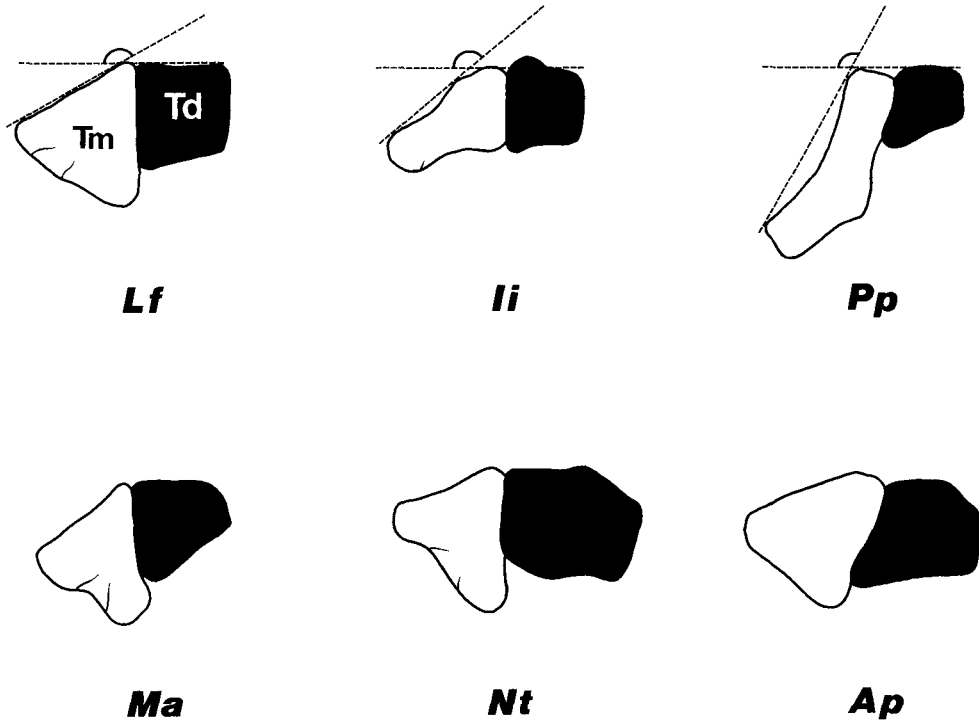


Fig. 6. Dorsal view of the articulated trapezium (Tm) and trapezoid (Td, shaded) of extant strepsirhines (**top row**) and adapiforms (**bottom row**). Note the expanded and divergent trapezium (Tm) of *Perodicticus potto* (Pp) and *Indri indri* (Ii) and slightly divergent and relatively unexpanded trapezium of *Lemur fulvus* (Lf), the Messel adapiform (Ma) (SMF-ME 1683), *Notharctus tenebrosus* (Nt) (AMNH 127167), and *Adapis parisiensis* (Ap) (RD 311). Not to scale.

among the extant locomotor groups studied (Table 1) in relative height of the pisiform body. The more pronograde taxa share a tall pisiform body, whereas the clingers and climbers have a pisiform that is not so rod-like (Figs. 3, 7; Tables 3, 4). Bivariate and univariate plots demonstrate that the adapiforms *Smilodectes*, *Notharctus*, and *Adapis* are most similar in relative pisiform height to quadrupedal anthropoids and prosimians. Based on their carpal size values, predicted pisiform height values were generated for each fossil specimen from each regression (Fig. 7; Table 5). The actual pisiform height values for all three adapiforms are well within the 95% prediction limits of the prosimian quadruped regression and quite close to the values predicted by the quadrupedal anthropoid regression (Table 5). Hence,

based on carpal size, pisiform height of these three adapiforms approximates what we would predict for an arboreal, quadrupedal primate.

Notably, prosimian quadrupeds differ from anthropoid quadrupeds in having a relatively shorter pisiform body (Tables 3, 4; Fig. 7). Prosimian quadrupeds might not require an FCU moment arm as powerful as that of anthropoid arboreal quadrupeds because they use leaping more often as a mode of displacement rather than frequent quadrupedal walking and running like monkeys. Godinot and Beard (1991, p. 316) remarked that "the influence of leaping on notharctine hand anatomy is not at all apparent." The smaller FCU moment arm of prosimian quadrupeds and notharctines compared to anthropoid quadrupeds may re-

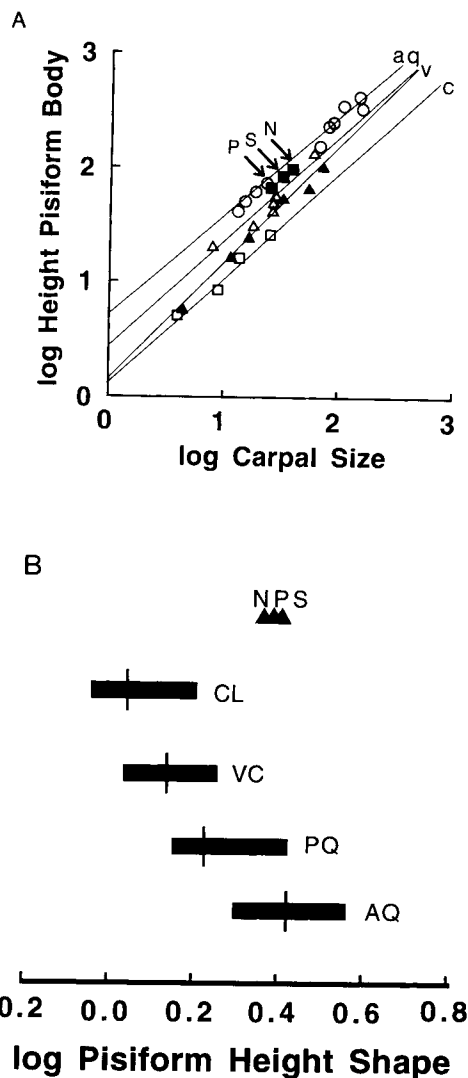


Fig. 7. **A:** Bivariate plot of mean species pisiform body height against carpal size for anthropoid quadrupeds (\circ ; a), prosimian quadrupeds (Δ ; q), vertical clingers (\blacktriangle ; v) slow climbers (\square ; c), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Smilodectes gracilis* (S) (USNM 13251), and *Notharctus tenebrosus* (N) (AMNH 127167). Lines represent Model I regression lines for each locomotor group. Male and female values for sexually dimorphic anthropoid taxa are plotted separately. **B:** Univariate plot of pisiform body height shape ratio values (log pisiform height/carpal size) for anthropoid quadrupeds (AQ), prosimian quadrupeds (PQ), vertical clingers (VC), slow climbers (CL), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Smilodectes gracilis* (S) (USNM 13251), and *Notharctus tenebrosus* (N) (AMNH 127167). The horizontal bars represent the distribution of species means for each locomotor group, and the vertical line is the median value for each group. Male and female values for sexually dimorphic anthropoid taxa are plotted separately.

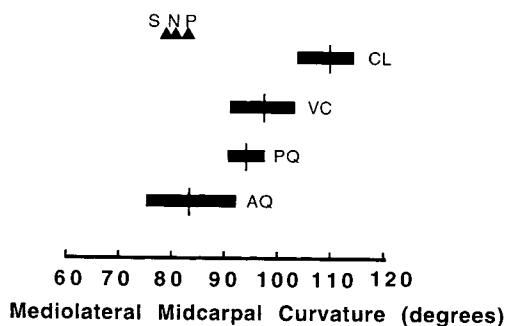


Fig. 8. Univariate plot of mediolateral midcarpal joint curvature values for anthropoid quadrupeds (AQ), prosimian quadrupeds (PQ), vertical clingers (VC), slow climbers (CL), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Smilodectes gracilis* (S) (USNM 13251), and *Notharctus tenebrosus* (N) (AMNH 127167). The horizontal bars represent the distribution of species means for each locomotor group, and the vertical line is the median value for each group. All measurements are in degrees. Male and female values for sexually dimorphic anthropoid taxa are plotted separately.

flect a preference for frequent leaping over quadrupedal walking and running.

A morphocline is also apparent among these extant locomotor groups in relative shape of the midcarpal joint, where the more quadrupedal taxa tend to have a flat midcarpal joint surface and the vertical clingers and climbers have a more tightly curved joint surface (Figs. 4, 8; Tables 3, 4). Quadrupedal prosimians and vertical clingers overlap considerably in this measure (Fig. 8; Table 4), although all three fossil specimens which preserve the morphology fall most closely within the range of variation for quadrupedal monkeys (Fig. 8). Godinot and Beard (1991) commented that *Notharctus* appears to possess a more proximally facing triquetrohamate facet than *Adapis* and *Smilodectes*, but these data (Figs. 4, 8) show that all three adapiforms are quite similar to one another in relative midcarpal joint curvature. The adapiform midcarpal joint appears to have served an important role in weight-bearing, in addition to allowing some radioulnar deviation.

The extant locomotor groups examined also differ significantly in relative dimensions of the thumb joint (Tables 3, 4). The vertical clingers and slow climbers have a radioulnarly expanded pollical carpometa-

TABLE 3. Results of analysis of covariance (ANCOVA) tests between extant primate locomotor groups in linear and angular carpal dimensions against carpal size¹

Comparison	Pisiform height	Midcarpal curvature	Trapezium breadth	Trapezium divergence
PQ v. VC	ns/* (VC > sl)	ns/ns	ns/* (VC > y)	*/ (PQ > sl)
PQ v. CL	ns/** (PQ > y)	ns/***	ns/** (CL > y)	ns/* (CL > y)
PQ v. AQ	ns/***	ns/***	ns/ns	ns/* (AQ > Y)
VC v. CL	ns/ns	ns/***	ns/* (CL > y)	ns/***
VC v. AQ	ns/***	ns/***	ns/** (VC > y)	ns/***
CL v. AQ	ns/***	ns/***	ns/***	ns/***

¹ Results are presented for ANCOVA slope test/y intercept test. AQ, anthropoid quadrupeds; CL, slow climbers; PQ, prosimian quadrupeds; VC, vertical clingers. Locomotor group sample sizes are shown in Table 1.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

ns, not significant.

TABLE 4. Results of pairwise comparisons between extant locomotor groups for log-shape variables, joint curvature, and thumb divergence values¹

Comparison	Log-pisiform height shape (K-W = 19.55, $P < .001$, 3 _{df})	Log-trapezium breadth shape (K-W = 18.67, $P < .001$, 3 _{df})	Midcarpal joint curvature (K-W = 19.62, $P < .001$, 3 _{df})	Thumb divergence (K-W = 17.85, $P < .001$, 3 _{df})
PQ v. VC	**	**	ns	ns
PQ v. CL	ns	***	***	***
PQ v. AQ	ns	ns	***	**
VC v. CL	ns	ns	***	***
VC v. AQ	***	***	***	***
CL v. AQ	***	***	***	***

¹ Results of Kruskal-Wallis tests (K-W) are shown in parentheses. AQ, anthropoid quadrupeds; CL, slow climbers; PQ, prosimian quadrupeds; VC, vertical clingers. Locomotor group sample sizes are shown in Table 1.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

ns, not significant.

carpal articulation, whereas that of the quadrupedal monkeys and prosimians is not so large relative to carpal size (Fig. 9). The actual trapezium breadth value for *Notharctus* is so low relative to carpal size that it is outside the 95% confidence limits of trapezium breadth values predicted by each locomotor group regression (Table 6). The actual trapezium breadth value for *Adapis* is closest to that predicted by the anthropoid quadruped regression, whereas the actual value for *Smilodectes* is closest to that predicted by the prosimian quadruped regression (Table 6). Similar results are obtained when trapezium breadth is expressed as a shape ratio (Fig. 9). These results indicate that all adapiforms, particularly *Notharctus*, pos-

sess relatively unexpanded pollical carpometacarpal articulations. This suggests that the thumb joints of adapiforms were not specialized for powerful and frequent pollical grasping like those of extant vertical clingers and lorisine slow climbers.

Prosimian slow climbers, and to a lesser extent vertical clingers, also have a first carpometacarpal articulation that is very divergent relative to the second carpometacarpal facet (Figs. 6, 10; Tables 3, 4). In contrast, the pollical carpometacarpal articular facet of quadrupedal anthropoids is not so divergent relative to the trapezoid (Fig. 10). The adapiforms resemble prosimian quadrupeds, and even vertical clingers somewhat, in relative thumb divergence, whereas the

TABLE 5. Actual values, predicted values, and 95% confidence limits (C.L.) of predicted values for adapiform relative pisiform height predicted from adapiform carpal size using quadrupedal prosimian, vertical clinger, slow climber, and quadrupedal anthropoid regression equations¹

Locomotor group	Taxon	Actual	Predicted	95% C.L.
Quadrupedal prosimians $Y = .92(X) + .37$				
	<i>Notharctus</i>	1.98	1.84	1.67–2.01
	<i>Smilodectes</i>	1.91	1.76	1.62–1.90
	<i>Adapis</i>	1.81	1.67	1.54–1.80
Vertical clingers $Y = 1.03(X) + .08$				
	<i>Notharctus</i>	1.98	1.72	1.62–1.82
	<i>Smilodectes</i>	1.91	1.64	1.55–1.73
	<i>Adapis</i>	1.81	1.54	1.46–1.62
Slow climbers $Y = .91(X) + .13$				
	<i>Notharctus</i>	1.98	1.58	1.37–1.79
	<i>Smilodectes</i>	1.91	1.51	1.32–1.70
	<i>Adapis</i>	1.81	1.42	1.26–1.58
Anthropoid quadrupeds $Y = .89(X) + .63$				
	<i>Notharctus</i>	1.98	2.05	2.00–2.10
	<i>Smilodectes</i>	1.91	1.98	1.93–2.03
	<i>Adapis</i>	1.81	1.89	1.84–1.94

¹ Fossil specimen numbers are shown in Fig. 3. Values are expressed in logarithmic units.

TABLE 6. Actual values, predicted values, and 95% confidence limits (C.L.) of predicted values for adapiform relative trapezium breadth predicted from adapiform carpal size using quadrupedal prosimian, vertical clinger, slow climber, and quadrupedal anthropoid regression equations¹

Locomotor group	Taxon	Actual	Predicted	95% C.L.
Quadrupedal prosimians $Y = .96(X) + .06$				
	<i>Notharctus</i>	1.32	1.59	1.51–1.66
	<i>Smilodectes</i>	1.54	1.52	1.45–1.59
	<i>Adapis</i>	1.38	1.42	1.38–1.46
Vertical clingers $Y = .99(X) + .13$				
	<i>Notharctus</i>	1.32	1.71	1.62–1.80
	<i>Smilodectes</i>	1.54	1.63	1.57–1.69
	<i>Adapis</i>	1.38	1.53	1.45–1.61
Slow climbers $Y = .77(X) + .53$				
	<i>Notharctus</i>	1.32	1.76	1.43–2.09
	<i>Smilodectes</i>	1.54	1.70	1.41–1.99
	<i>Adapis</i>	1.38	1.62	1.41–1.83
Anthropoid quadrupeds $Y = .99(X) - .04$				
	<i>Notharctus</i>	1.32	1.54	1.47–1.61
	<i>Smilodectes</i>	1.54	1.46	1.38–1.54
	<i>Adapis</i>	1.38	1.36	1.28–1.80

¹ Fossil specimen numbers are shown in Fig. 3. Values are expressed in logarithmic units.

Messel adapiform has an especially divergent thumb (Figs. 6, 10). These results support previous observations (Godinot and Beard, 1991; Godinot, 1991; Franzen, 1993) that adapiforms have a divergent thumb much like those of arboreal prosimians. Trapezium divergence plays the first metacar-

pal opposite the postaxial rays so that arboreal substrates can be clasped between the thumb and ulnar digits. Furthermore, trapezium divergence enables the first metacarpal to move transversely across the palm when it is flexed. Hence, the thumb of adapiforms was quite capable of grasping arboreal

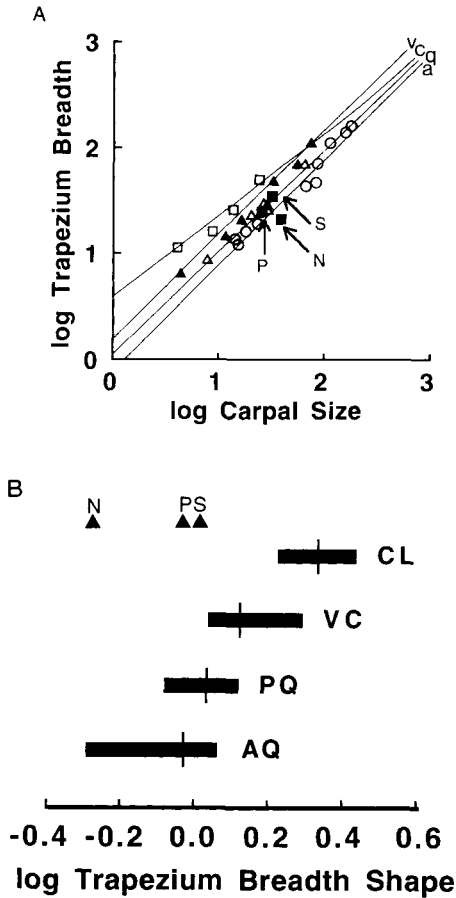


Fig. 9. **A:** Bivariate plot of mean species trapezium articular breadth against carpal size for anthropoid quadrupeds (\circ ; a), prosimian quadrupeds (Δ ; q), vertical clingers (\blacktriangle ; v), slow climbers (\square ; c), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Smilodectes gracilis* (S) (USNM 13251), and *Notharctus tenebrosus* (N) (AMNH 127167). Lines represent Model I regression lines for each locomotor group. Male and female values for sexually dimorphic anthropoid taxa are plotted separately. **B:** Univariate plot of trapezium articular breadth shape ratio values (log trapezium breadth/carpal size) for anthropoid quadrupeds (AQ), prosimian quadrupeds (PQ), vertical clingers (VC), slow climbers (CL), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Smilodectes gracilis* (S) (USNM 13251), and *Notharctus tenebrosus* (N) (AMNH 127167). The horizontal bars represent the distribution of species means for each locomotor group, and the vertical line is the median value for each group. Male and female values for sexually dimorphic anthropoid taxa are plotted separately.

substrates of variable size and orientation. The thumb joints of these early primates, however, lack the great expansion characteristic of extant prosimian slow climbers and

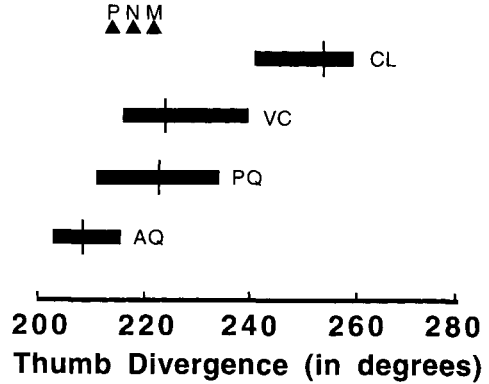


Fig. 10. Univariate plot of trapeziometacarpal divergence values for anthropoid quadrupeds (AQ), prosimian quadrupeds (PQ), vertical clingers (VC), slow climbers (CL), and the fossil adapiforms *Adapis parisiensis* (P) (RD 311), *Messel adapiform* (M) (SMF-ME 1683), and *Notharctus tenebrosus* (N) (AMNH 127167). The horizontal bars represent the distribution of species means for each locomotor group, and the vertical line is the median value for each group. All measurements are in degrees. Male and female values for sexually dimorphic anthropoid taxa are plotted separately.

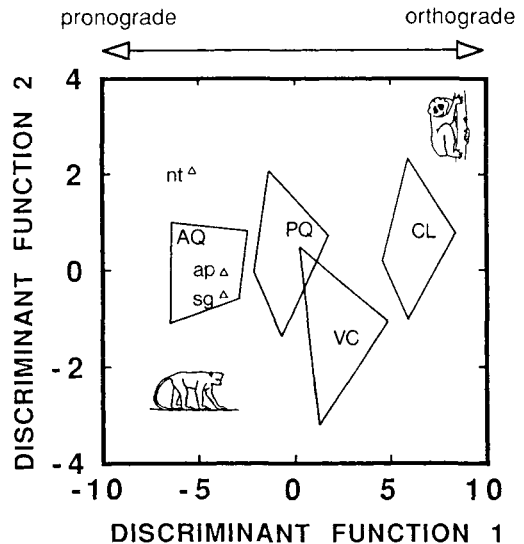


Fig. 11. Bivariate plot of the first two discriminant function axes for a discriminant analysis of carpal joint shape ratios and joint curvature values for anthropoid quadrupeds (AQ), prosimian quadrupeds (PQ), vertical clingers (VC), slow climbers (CL), and the fossil adapiforms *Adapis parisiensis* (ap) (RD 311), *Smilodectes gracilis* (sg) (USNM 13251), and *Notharctus tenebrosus* (nt) (AMNH 127167). The polygons enclose the range of locomotor group mean species values. Male and female values for sexually dimorphic anthropoid taxa are plotted separately. Inset figures modified from Fleagle (1988).

TABLE 7. Correlations (loadings) between dependent variables and factor scores for each discriminant function axis of the discriminant function analysis shown in Figure 11.¹

Variables	Axis 1	Axis 2	Axis 3
MIDCV	0.60	0.20	-0.55
TZMDIV	0.57	0.64	0.31
PISH	-0.44	0.43	0.38
TZMW	0.40	0.05	0.77

¹ Abbreviations are as follows: MIDCV, mediolateral midcarpal joint curvature; PISH, dorsoventral height of the pisiform body; TZMDIV, divergence of the pollical carpometacarpal joint facet; TZMW, mediolateral breadth of the pollical carpometacarpal joint.

vertical clingers which use a pincer grasp (Forster, 1933, 1934; Jouffroy, 1993) (Figs. 6, 10).

A multivariate discriminant function analysis was also used to both test for differences in carpal joint morphology between extant locomotor groups and identify the group which each adapiform is closest to in carpal morphology. The discriminant function classified 95% of the extant cases correctly, was highly significant ($P < .001$; Wilkes-Lambda), and assigned all three fossil specimens to the quadrupedal anthropoid group (Fig. 11). The first discriminant function separates those extant taxa which frequently engage in more orthograde postural and locomotor behaviors from those extant primates which use quadrupedal positional behaviors more often (Fig. 11). Specifically, the vertical clingers and slow climbers have positive factor scores on this axis, and the quadrupedal anthropoids and prosimians have negative scores (Fig. 11). The adapiform taxa, like quadrupedal anthropoids, all have very low scores on the first axis (Fig. 11).

The first discriminant axis shows a strong positive correlation with midcarpal curvature and trapezium divergence (Table 7), indicating that the slow climbers and clingers have a high degree of midcarpal curvature and a very divergent thumb (Fig. 11). The slow climbers have higher scores on this axis than vertical clingers because they have a greater degree of midcarpal curvature related to increased radioulnar mobility at the wrist for climbing. This again relates to the observation that orthograde locomotor behaviors require increased wrist joint mobility compared to orthograde postural behaviors (Hamrick, 1996). This axis also shows

a strong negative correlation with pisiform height (Table 7), illustrating that the climbers and clingers have high scores and a small pisiform, whereas the quadrupeds have low scores and a large pisiform (Fig. 11). These multivariate results underscore prior univariate and bivariate analyses, which show that the carpal joints of early Tertiary adapiform primates are most similar to those of living quadrupedal primate taxa.

DISCUSSION

Results presented here expand upon previous studies of adapiform postcranial anatomy by evaluating adapiform carpal morphology qualitatively and quantitatively within the context of extant morphoclines in carpal joint shape. The behavioral repertoires inferred for *Adapis*, *Notharctus*, and the Messel adapiform include frequent quadrupedalism and in this way resemble the reconstructions of Godinot and Jouffroy (1984), Godinot and Beard (1991), and Franzen (1993). Furthermore, this study shows that *Adapis* and *Notharctus* resemble one another in mechanically significant ulnocarpal and midcarpal joint features, although *Notharctus* exhibits a pollical carpometacarpal joint that is less expanded than those of other adapiforms and extant primates. These comparative data also illustrate that the Messel adapiform shares similarities in wrist morphology with extant vertical clingers, such as a medially facing triquetrohamate facet and relatively expanded thumb joint.

Perhaps the most surprising result of this analysis is that *Smilodectes* also resembles quadrupedal monkeys and prosimians in carpal joint morphology. These results contrast with those derived from earlier studies of the *Smilodectes* forelimb, which presented evidence for similarities in elbow (Szalay and Dagosto, 1980), shoulder (Covert, 1985a,b; Schmitt 1991, in press), and carpal (Godinot and Beard, 1991) morphology between *Smilodectes* and extant vertical clingers. Evidence provided by this study shows that *Smilodectes* resembles *Notharctus* and *Adapis* in aspects of wrist morphology, such as dimensions of the pisiform body, midcarpal articulation, and pollical carpometacarpal joint, which are functionally related to

quadrupedal, palmigrade arboreal locomotion.

These data on carpal form also reveal some interesting contrasts in hand morphology between anthropoids and prosimians. The quadrupedal anthropoids studied have a taller pisiform body, flatter midcarpal surface, and reduced trapeziometacarpal articulation compared to those extant prosimians which also prefer locomotion on horizontal substrates (Figs. 7–9). Adapiforms resemble quadrupedal monkeys in the relative expression of these traits more so than quadrupedal prosimians (Fig. 11). Recent studies (Beard et al., 1988; Beard and Godinot, 1988; Covert and Williams, 1994; Dagosto and Gebbo, 1994; Ross, 1994) have suggested that adapiforms are the sister group of extant strepsirhines. If this scenario is correct, then extant strepsirhine quadrupeds, vertical clingers, and slow climbers evolved an expanded thumb joint, more mediolaterally curved midcarpal joint, and smaller pisiform body after the divergence of adapiform primates.

Alternatively, the similarities between adapiforms and monkeys could be viewed as evidence of a close phylogenetic relationship between the two groups, which has been suggested by other workers (e.g., Rasmussen, 1986, 1990, 1994; Franzen, 1994). A reduced trapezium, flat midcarpal joint, and tall pisiform body are also found in most scandentians, insectivores, and rodents, which indicates that the similarities shared between these two groups are most likely primitive for primates as a whole (Hamrick, 1995). Adapiforms and monkeys may then possess a number of carpal features which are primitive for the Order Primates. A complete analysis of the morphological transformations which have characterized early primate carpal evolution is in progress. The preliminary results presented here, however, suggest that extant strepsirhines are quite derived in many carpal features relative to both living monkeys and early Tertiary primate taxa.

CONCLUSIONS

Early Tertiary adapiform primates share with living arboreal quadrupeds 1) a tall pi-

siform body, 2) a mediolaterally (= radioulnarly) flat midcarpal joint surface, and 3) a relatively unexpanded first metacarpal articular facet. Functionally, these features of the adapiform wrist are related to 1) extending (= dorsiflexing) the proximal carpal joint during quadrupedal locomotion, 2) increasing midcarpal joint stability during quadrupedal, weight-bearing postures, and 3) grasping arboreal substrates during arboreal positional behaviors. Furthermore, adapiforms have a small hamate hamulus like extant quadrupedal monkeys, indicative of a relatively shallow carpal tunnel. This suggests adapiforms possessed extrinsic digital flexors that were apparently not so well developed as those of living strepsirhine quadrupeds, clingers, and climbers. Adapiforms resemble most quadrupedal prosimians, and some prosimians which practice vertical clinging, in having a divergent pollical carpometacarpal articulation. The divergent thumb of adapiforms indicates that they were clearly arboreal, but their carpal joints lack mechanical adaptations for habitual vertical clinging and/or slow climbing. Similarities in carpal form between adapiforms and quadrupedal monkeys functionally related to wrist extension, pronation, and weight-bearing suggest that some form of arboreal, pronograde locomotion characterized the common ancestor of both prosimians and anthropoids.

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